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THE GENERA OF LOGANIACEAE IN THE  
SOUTHEASTERN UNITED STATES<sup>1</sup>

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LOGANIACEAE C. F. P. Martius, Nov. Gen. Sp. Pl. Brasil. 2: 133. 1827,  
"Loganieae," nom. cons.

(LOGANIA FAMILY)

Shrubs [trees] or vines, rarely herbs. Trichomes unicellular, uniseriate, or with a variable, multicellular, broadened head (mostly confined to the *Buddlejeae*), or candelabrum shaped (only *Buddlejeae*). Leaf bases, stipules, bracts,

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Dorothy H. Marsh drew the illustrations in May, 1957, under the supervision of R. B. Channell and C. E. Wood, Jr. The figures are based on specimens in the herbaria of the Arnold Arboretum and Gray Herbarium and on spirit-preserved materials collected by R. B. Channell and H. F. L. Rock. Donna Rogers, my wife, is thanked for translating literature from French. Reviews of the manuscript by C. E. Wood, Jr., and N. G. Miller yielded improvements, as did E. B. Schmidt's and S. A. Spongberg's editorial efforts. Barbara Nimblett moved the project along quickly by performing much of the typing.

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and calyces often with colleters adaxially. Leaves usually opposite or infrequently whorled or pseudowhorled [or rarely alternate], simple, entire or toothed [to infrequently lobed], penninerved or with ascending, arcuate lateral nerves, or vasculature other than the midrib inconspicuous in reduced leaves. Stipules diverse, interpetiolar (then leafy, membranaceous, or reduced to a ridge or flange) or rarely represented by a pair of lobes flanking each petiole. Inflorescences terminal (then sometimes in forks between branches) or axillary, fundamentally cymose but otherwise variable, sometimes dichasial, cincinnous (then often spicate), fasciculate, thyriform, scorpioid, or paniculiform, sometimes tightly congested, occasionally with solitary flowers; showy bracts lacking. Flowers mostly actinomorphic or somewhat zygomorphic, perfect or infrequently imperfect, tetramerous or pentamerous. Calyx lobes separate or coalescent, often unequal. Corolla tubular, cylindrical to funnelform or urceolate, with variously oriented imbricate, valvate [or contorted] lobes, the tube often occluded by hairs. Stamens typically alternating with same number of corolla lobes [or reduced in number], epipetalous, usually uniform; anthers introrse, dehiscent longitudinally; pollen grains usually colpate (to colpate in *Spigelia*). Ovary superior to partly inferior, usually bilocular (tetralocular in *Buddleja madagascariensis*) [or rarely unilocular or with 3–5 partial or complete locules], containing [1 to] many anatropous, hemianatropous, or reportedly amphitropous ovules in each locule on axile, frequently peltate [or rarely parietal or basal] placentae; stigmas unlobed, 2-lobed, or 4-lobed. Fruits usually capsules with septicial dehiscence predominant but also with varying degrees of loculicidal dehiscence, thus separating partly or completely into 2 (a pair of apical horns in some genera) or 4 segments [or infrequently loculicidal only], in some berries [or drupes]. Seeds usually numerous and small, winged or not, the embryo straight; endosperm initially nuclear or cellular [or intermediate], sometimes ruminant, surrounding the embryo; embryo sac (megagametophyte) of the Polygonum type. (Including Buddlejaceae Wilhelm, Samenpfl. 90. 1910, "Buddleiaceae," nom. cons.; Spigeliaceae Martius, Nov. Gen. Sp. Pl. Brasil. 2: 132. 1827.) TYPE GENUS: *Logania* R. Brown, nom. cons.

As recently defined by Leeuwenberg & Leenhouts (to embrace the Buddlejaceae), a family of 29 genera and about 470 species in ten tribes distributed pantropically and subtropically with limited extensions into the temperate zones. The two largest genera, *Strychnos* L. and *Buddleja* L., are pantropical and contain between 90 and 200 species each. Seven genera grow free of cultivation in the continental United States. *Emorya suaveolens* Torrey, the sole species of its genus, is endemic to northern Mexico and southern Texas. The cultivated *Strychnos spinosa* Lam. escapes infrequently to disturbed places in Florida. As elaborated later, at least one species of *Buddleja* is naturalized in the southeastern United States, and species of *Mitreola* L. (*Cynoctonum* J. F. Gmelin), *Polypremum* L., *Spigelia* L., and *Gelsemium* Juss. are indigenous in the range of the Generic Flora.

The comprehensive treatment in the second edition of *Die Natürlichen Pflanzenfamilien* (1980) contains a taxonomic revision at the generic level (Leeuwenberg & Leenhouts) and stands as the principal modern work on the Loganiaceae. See Klett and Solereder (1892) for earlier revisions.

Broadly interpreted, the family is characterized, with exceptions, by opposite leaves with interpetiolar stipules (or sheaths, flanges, or ledges), fundamentally cymose inflorescences, actinomorphic (or weakly zygomorphic), tetramerous or pentamerous flowers, epipetalous stamens alternating with the lobes of the tubular corolla, and superior (or in some partly inferior), generally bilocular ovaries most often enclosing axile (sometimes peltate) placentae bearing numerous ovules. The seeds contain straight embryos. Most genera, other than *Buddleja*, its allies, and some others, have internal phloem and vested pits on the vessel elements.

The subdivision, delimitation, and position of the Loganiaceae are long-standing problems. The family has been an artificial "catchall" for difficult-to-place genera. Moreover, it is relatively poor in obvious specialized characters and thereby resembles the ancestral stock from which related families arose. The Loganiaceae also show multiple links between their heterogeneous subunits and other families. Extreme taxonomic views have been to splinter the Loganiaceae into several smaller families (e.g., see Hutchinson) or to apportion its major components among related families (e.g., see Bureau).

Modern authors generally place the Loganiaceae in the inconsistently circumscribed order Gentianales (Contortae), with the Apocynaceae, Gentianaceae, and Rubiaceae receiving most attention as probable close relatives. The tribe Buddlejeae spans an ordinal boundary in that it shows similarities to the Scrophulariales (Tubiflorae).

The Loganiaceae *sensu stricto* and the Rubiaceae share several characters—interpetiolar stipules, colleters, wood sometimes accumulating aluminum and usually with vested pits, pollen with similar wall stratification (Cronquist), and nuclear endosperm. The two families are further bound together, along with the Apocynaceae, by their tryptophan-tryptamine indole alkaloids (see Kisakürek *et al.*). With exceptions, the Rubiaceae differ from the Loganiaceae *sensu stricto* in their inferior ovaries and lack of internal phloem. (See discussion of the tribe Spigeliae below for one narrow gap between the Loganiaceae and the Rubiaceae.)

In their study of tryptophan-tryptamine indole alkaloids, Kisakürek and colleagues found that the Loganiaceae overlap even more with the Apocynaceae than with the Rubiaceae, and that they appear to be less specialized than either of these two families. The Apocynaceae and Loganiaceae both have internal phloem, vested pits, nuclear endosperm, and colleters. Differences are that the Apocynaceae have a latex system (but note that the loganiaceous *Fagraea* Thunb. produces latex in fruits), mostly lack stipules, and tend to have both androecial and gynoecial specializations.

Similarities between the Gentianaceae and the Loganiaceae include internal phloem, colleters, xanthones, usually nuclear endosperm, and wood that sometimes accumulates aluminum (Cronquist; Bisset, 1980a). There are close morphological similarities. The Gentianaceae differ in lacking stipules (although interpetiolar flanges occur) and, with exceptions in both families, in having unilocular ovaries with parietal placentae.

*Buddleja* belongs to a collection of about seven genera of uncertain placement. Authors who give this group membership in the order Gentianales either treat

it as a family (e.g., Thorne) or assign it an infrafamilial rank in the Loganiaceae. Leeuwenberg & Leenhouts treated it as tribe Buddlejeae in the Loganiaceae, the rank and position adopted tentatively in the present paper. When placed in the order Scrophulariales (Tubiflorae), the Buddlejeae have been included in the Scrophulariaceae by some botanists, but most who advocate this ordinal placement (e.g., Cronquist, Melchior, Takhtajan) accept the separate family Buddlejaceae.

Taxonomic alignment of the Buddlejeae with the Loganiaceae rests largely upon transitional genera and a few morphological characters, in particular presence of stipules and actinomorphic or weakly zygomorphic corollas. On the other hand, most genera of the Buddlejeae stand apart in their lack of colleters, internal phloem, and vestured pitting (also absent in *Gelsemium* and a small number of other nonbuddlejaceous genera; see Mennega). They further stand apart in having pericyclic (vs. superficial) cork (*Peltanthera* Benth, nom. cons., and probably *Sanango* Bunting & Duke are exceptions in the Buddlejeae), endothelium in the ovule, cellular (vs. generally nuclear) endosperm, chromosome numbers based mostly on 19, complex trichomes with laterally adjacent cells making up broadened heads or tiers (vs. trichomes usually unicellular or uniseriate), an inconsistent tendency toward serrate leaves, and frequently tetramerous (vs. pentamerous) flowers having imbricate (vs. usually contorted or valvate) corolla lobes. (*Peltanthera* and *Sanango* are pentamerous exceptions in the Buddlejeae, and *Peltanthera* and *Buddleja* sometimes have valvate corolla lobes. Imbricate lobes appear in the Spigeliae in *Mitreola*.)

Intermediate genera complicate severing the Buddlejeae from the rest of the Loganiaceae. *Mitrasacme* Labill., which is usually placed in the Spigeliae, approaches the Buddlejeae in having intermediate endosperm and, reportedly, pericyclic cork in the root (Morelle). (Records of glandular trichomes in *Mitrasacme* are of dubious accuracy.) The somewhat similar and likewise intermediate genus *Polypremum* is discussed below.

*Peltanthera* and *Sanango*, especially, seem to approach the tribe Antonieae Endl. (Leenhouts, 1963). Leeuwenberg (1975) perceived similarities between *Nuxia* Lam., other genera of the Buddlejeae, and the tribe Antonieae in the capsule, endosperm, and embryo. Klett and Bunting & Duke stressed that *Logania* resembles the Buddlejeae.

Developmental evidence led Hasselberg (also see Weberling) to challenge the presumed homology between stipules in the Buddlejeae and other Loganiaceae; more work, however, is needed.

Affinity of the Buddlejeae with the Scrophulariaceae and other Scrophulariales is an old concept that is still sustained largely by embryological and chemical characters. Embryologically, the Buddlejeae agree far better with the Scrophulariales than with the other Loganiaceae (see Wagenitz, 1959; Dop; Davis); still, cellular endosperm and endothelia are widespread among flowering plants and sampling is spotty. Palynology has been invoked to support a scrophularian alignment (see Punt & Leenhouts), but after broadened sampling Punt (1980) concluded that palynology failed to support a relationship of the Buddlejeae with other tribes of the Loganiaceae.

In producing aucubins and related iridoids instead of seco-iridoids, *Buddleja* resembles the Scrophulariaceae and allies while diverging from several genera of the Loganiaceae and other Gentianales. Flavone 6-hydroxyluteolin and other flavonoids point *Buddleja* toward a scrophularian position. In a paper in which they documented this, Harborne & Williams used the similar compound scutellarein to tie the Plantaginaceae to the Tubiflorae (Scrophulariales) before Marin and colleagues (under *Buddleja*) isolated a glucoside of scutellarein from *B. globosa* Hope. Harborne (p. 287) mentioned crocein as "yet another [flavonoid] link between *Buddleja* and the Scrophulariaceae" and listed orobanchin and similar substances in *Buddleja*, *Catalpa* (Bignoniaceae), *Verbascum* (Scrophulariaceae), *Orobanche* (Orobanchaceae), and *Syringa* (Oleaceae). Weaknesses in the chemical evidence are that aucubins and similar compounds, as well as 6-hydroxylated flavones, including 6-hydroxyluteolin and scutellarein, have been detected in disparate families such as the Eucommiaceae, Rosaceae, Rubiaceae, and Compositae quite removed from the Scrophulariaceae. (For further discussion of the chemical data, see Daniel & Sabnis; Bisset, 1980a; and Jensen *et al.*)

Taxonomically selective pests add further links between *Buddleja* and the Scrophulariaceae. A leaf-mining fly and two species of weevils thought to attack only the latter transfer to *Buddleja*, and a species of the fungal genus *Peronospora*, otherwise restricted to hosts in the Scrophulariaceae, has been found on *B. globosa*. (The fungus on the *Buddleja* has been treated as a distinct species, however.) (See Hering; Mohrbutter; Wagenitz, 1959; and Williams, under *Buddleja*, for more on this line of evidence.)

According to Cronquist (p. 947), Piechura showed "strong serological affinities between the Buddlejeae and several tested families of Scrophulariales." The irregular pentamerous flowers of *Sanango* (*Gomara*) with four (nondidymous) fertile stamens and a sterile staminode further attracted Cronquist's attention as a similarity between the Buddlejeae and the Scrophulariales (also pointed out by Bunting & Duke).

For discussion of the possible relationship between the Buddlejeae and the Scrophulariales, see Hakki, Hasselberg, Hunzicker & Di Fulvio, Leenhouts (1963), Solereder (1892), Tiagi & Kshetrapal, and Wagenitz (1959); under *Buddleja* see Souèges.

Altogether, the Buddlejeae seem bound to the other Loganiaceae by intermediate genera and very weakly by the widespread as well as questionably homologous characteristics of stipules and actinomorphy, while they differ in numerous but overlapping features. *Buddleja*, and to an uncertain extent the other Buddlejeae, resemble the Scrophulariales in a set of widespread embryological characteristics and in chemical traits, all of which are too generalized to be trusted without reservation. Sampling remains disconcertingly skimpy for the difficultly evaluated characters.

Students of the Loganiaceae gather *Spigelia*, *Mitreola*, *Mitrasacme*, and sometimes *Polyprenum* together either as an infrafamilial taxon of varying rank or as a separate family. Leeuwenberg & Leenhouts recognized this assemblage, including *Polyprenum*, as the tribe Spigeliaceae. With exceptions the following characters help to unite the tribe: herbaceous growth; pseudodichoto-

mous-dichasial branching; arcuate foliar nerves; cincinnous units in the inflorescences; thin corollas; partly inferior ovaries (superior in *Spigelia*); peltate, rounded seeds on peltate placentae; and apically bilobed capsules of questionable homology. Palynological evidence, however, is divisive, except that the pollen tends to be oblate (Punt, 1980). Punt (1980) found each of four main pollen types within the Spigeliaceae to agree best with genera outside the tribe.

The capsular fruits offer the most convenient distinctions between genera of the Spigeliaceae. Those of *Spigelia* are markedly bilobed apically with the uniquely articulated style inserted in the cleft between the lobes. The capsules dehisce to leave behind cuplike or boatlike bases on the plant (see FIGURE 1j). As the capsule matures in *Mitreola* and *Mitrasacme*, the upper portion of the two carpels separates into a pair of horns that open longitudinally face to face. Either separation of the horns splits the style lengthwise, or the style remains partly intact apically and bridges the horns; occasionally the style remains completely intact on one horn (see FIGURE 2e). Many undehisced capsules of *Polypreum* slightly resemble those of *Spigelia* in being indented apically; upon dehiscence they appear a little like those of *Mitreola* and *Mitrasacme*, parting into a pair of apical lobes, each of which opens along adaxial lines. In *Polypreum*, however, both the abaxial and the adaxial walls tend to open, the apical lobes are not as distinctly or as precociously developed as the horns in the other two genera, and the style remains whole.

Flowers in the Spigeliaceae are pentamerous (*Mitreola*, *Spigelia*) or tetramerous (*Polypreum*, *Mitrasacme*) and have imbricate (*Polypreum* and sometimes *Mitreola*) or more or less valvate aestivation (*Spigelia*, *Mitrasacme*, and sometimes *Mitreola*). *Mitrasacme* (with exceptions), *Mitreola*, and *Polypreum* have partly inferior ovaries, as opposed to superior ovaries in *Spigelia*. The flowers are borne along cincinnous branches in *Mitreola*, most species of *Spigelia* (in others flowers are few in monochasia or in small, essentially monochasial pseudoumbellate clusters), and infrequently in *Polypreum* (where they are also arranged singly between dichasial branches or otherwise). Flowers of *Mitrasacme* are either solitary or in pseudoumbellate cymes.

Vegetative traits are least useful for distinguishing genera of the Spigeliaceae. Leaves often in rosettes help to set *Mitrasacme* apart from *Mitreola*. Extensive pseudodichotomous-dichasial branching, sprawling or broomlike habit, various scabrous-serrulate organs, and nearly linear leaves characterize, but are not unique to, *Polypreum*.

Modern botanists agree that the placement of *Polypreum* in the Rubiaceae is incorrect (see Moore under *Polypreum*; see also Punt & Leenhouts), but its position in the Spigeliaceae is not free from controversy. Assignment to the Buddlejaceae is plausible.

As justification for numbering *Polypreum* among the Spigeliaceae, Leenhouts (1962) listed its herbaceous habit, membranaceous interpetiolar stipular sheaths (also found in Buddlejaceae), partly inferior ovaries, and nearly basal peltate placentae (vs. placentae usually axile in Buddlejaceae, except *Peltanthera*, which in published illustrations appears to have more or less peltate placentae). Additional features to be found with varying degrees of prevalence in both *Polypreum* and the Spigeliaceae are reduced leaves (reappearing in the Buddlejaceae),

pseudodichotomous-dichasial branching, flowers in cincinni, seeds broader than long and attached peltately (vs. usually elongate and attached at the ends in the Buddlejeae, but note that seeds much like those of *Polypreum* are found in *Gomphostigma* and rarely in *Buddleja*), palisade parenchyma in the stem (see Morelle for this in *Spigelia*), and superficial initiation of cork. (For a report of superficial cork in *Polypreum*, see Metcalfe & Chalk.) Cork is pericyclic in members of the Buddlejeae, except *Peltanthera*. Morelle reported an exceptional instance of cork forming deep in the cortex in *Spigelia* and in the root in *Mitrasacme*. Vegetatively, *Polypreum* is especially reminiscent of *Mitrasacme*, some species of which, moreover, have tetramerous flowers much like those of *Polypreum*. Capsules not much different from those of *Polypreum* occur in *Mitreola*. (The vegetative habit, flower, and capsules of *Polypreum* could, nevertheless, be readily accommodated in the Buddlejeae.) Punt & Leenhouts interpreted palynological evidence to indicate *Polypreum* as closer to the Spigeliaceae. (Punt, 1980, later concluded that *Polypreum* resembles *Mitrasacme* palynologically but is even more like *Strychnos*.)

*Polypreum* resembles genera of the Buddlejeae more than genera of the Spigeliaceae in having trichomes with broadened multicellular heads. Yet there exist a few indications of hairs with multicellular heads in the Spigeliaceae: the "stellate hairs" of some species of *Spigelia* differ in structure from other types of trichomes under consideration here, although Hurley's mention of multicellular glandular hairs in this genus warrants further checking. Reports of complex hairs in *Mitrasacme* are probably wrong. Further points of resemblance between *Polypreum* and the Buddlejeae are the integumentary tapetum (endothelium) in the ovule (but this uniquely becoming the principal hardened layer in the seed coat in *Polypreum*), cellular endosperm (vs. endosperm nuclear or intermediate in the Spigeliaceae), possible possession of the flavone scutellarein (Harborne & Williams; Marin *et al.*, under *Buddleja*), and chromosomal size and morphology (Moore, 1947). *Polypreum* and the Buddlejeae depart from the Spigeliaceae in lacking colleters, internal phloem, and vested pitting. For the last two characters at least one examination is either recorded in the literature or has been made in the course of preparing this paper for all genera of Spigeliaceae. In the Buddlejeae *Buddleja*, *Sanango*, and *Peltanthera* have been checked for internal phloem; the nature of pitting in vessel elements has been verified for all except *Sanango*. (I used a scanning electron microscope to examine pitting on vessel elements from every genus of the Spigeliaceae and from *Peltanthera*, *Buddleja*, and *Emorya* in the Buddlejeae.) The generalized or negative nature of most of the characters cited in connection with the placement of *Polypreum* leaves few obvious specializations shared with either set of potentially closest relatives.

If members of the Spigeliaceae belong together, they may be most closely related to members of the tribe Loganieae, as hinted by limited resemblances in cytology (Gadella), wood anatomy (Mennega), and morphology (Leeuwenberg & Leenhouts).

In view of the suspected proximity of the Loganiaceae and the Rubiaceae, it is of interest to note that members of the Spigeliaceae and the rubiaceous tribe Hedyotideae show dichasial branching, interpetiolar stipules, colleters, arcuate

foliar nerves, similarities in wood anatomy (Mennega), partly inferior ovaries containing numerous, often peltate ovules on stalked placentae, resemblances in floral vasculature (Tiagi & Kshetrapal), small, sculptured seeds, and markedly two-parted capsules (these sometimes bilobed apically and dehiscent both loculicidally and septocidally). *Mitrasacmopsis* Jovet is an intermediate genus generally placed in the Rubiaceae, although it resembles *Mitrasacme*.

The Spigeliaeae differ from the Hedyotideae palynologically, as well as in having internal phloem (lacking in *Polypremum*) and in (usually?) lacking raphides (but see Morelle, and Holm (1907, under *Spigelia*)).

Various members of the Loganiaceae are used as ornamentals and as sources of drugs, poisons, and medicines. Among those cultivated in warm-temperate and tropical gardens are *Strychnos spinosa* (Natal orange), species of *Spigelia*, *Gelsemium sempervirens*, *Nuxia floribunda* Benth., *Desfontainia spinosa* Ruiz & Pavón, species of *Fagraea*, *Geniostoma ligustrifolium* A. Cunn., and over 25 species, cultivars, and hybrids of *Buddleja*. A few species of *Buddleja* are hardy in cool-temperate gardens. Foremost among the genera that yield bioactive substances is *Strychnos*, a genus well known for its wealth of alkaloids, in addition to iridoids, saponins, and no doubt other compounds with toxic or pharmacological potency. Species of *Strychnos* yield fish poisons, folk remedies, and drugs. Derivatives are ingredients in curares, from which indirectly came the surgical muscle-relaxant alcuronium. Other alkaloidal drugs from *Strychnos* are brucine and strychnine (the latter most familiar as a rat poison). *Strychnos potatorum* L. f. clears turbid water. (For a review of uses for Loganiaceae, see Bisset, 1980b.)

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- . Notes on American Loganiaceae. V. Key to the genera represented in America. *Acta Bot. Neerl.* **20**: 539–542. 1971. [Includes list of tribes.]
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- . The Loganiaceae of Africa XIV. A revision of *Nuxia* Lam. *Meded. Landb. Wageningen* **75**(8): 1–80. 1975. [This genus shows affinities in capsule, endosperm, and embryo to the loganiaceous tribe Antonieae and is close to *Buddleja* and relatives.]
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- MOORE, R. J. Cytotaxonomic studies in the Loganiaceae. I. Chromosome numbers and phylogeny in the Loganiaceae. *Am. Jour. Bot.* **34**: 527–538. 1947. [Includes illustrations of chromosomes in *Gelsemium sempervirens*, *Polypreum procumbens*, *Spigelia marilandica*, and all of our species of *Buddleja*; also includes distribution map for *Buddleja*, taxonomic history of the family, and discussion of familial relationships; chromosome numbers determined for 24 species in seven genera plus 17 variants of *B. Davidii*.]
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- PERRY, L. M. (with the assistance of J. METZGER). Medicinal plants of East and Southeast Asia: attributed properties and uses. ix + 620 pp. Cambridge, Massachusetts, and London. 1980. [Loganiaceae, 243–245; includes *Gelsemium* and *Buddleja*; *B. Lindleyana* poisonous.]
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- . Pollen morphology [of Loganiaceae]. *Nat. Pflanzenfam.* ed. 2. **28bI**: 162–191. 1980. [See HOC & BRAVO (under *Spigelia*) for more recent survey of some genera that disagrees substantially with PUNT.]
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- STEFFEY, J. The logania family. *Am. Hort.* **60**(8): 4, 6, 7. 1981. [Species of *Buddleja*, *Gelsemium*, *Spigelia*, *Strychnos*, and *Fagraea* from the horticultural standpoint.]
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- & S. KSHETRAPAL. Studies on the floral anatomy, evolution of the gynoecium and relationships of the family Loganiaceae. *In*: Y. S. MURTY *et al.*, eds., *Advances in plant morphology* **1972**: 408–416. 1972 [1975]. [*Mitreola*, *Buddleja*, *Nicodemia*, and *Strychnos*; includes discussion of relationship between Rubiaceae and Loganiaceae (floral vasculature of *Mitreola* suggests Rubiaceae) and placement of Buddlejaceae.]
- TIREL-ROUDET, C. Loganiaceae. *Fl. du Cambodge, du Laos et du Vietnam* **13**: 3–89. 1972. [Includes *Gelsemium* (with distribution map for *G. elegans*) and *Mitreola*; Buddlejaceae treated separately by A. J. M. LEEUWENBERG & J. E. VIDAL, 90–97.]
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- VINES, R. A. *Trees, shrubs and woody vines of the Southwest*. xii + 1104 pp. Austin, Texas. 1960. [*Gelsemium* (*G. sempervirens* in Oklahoma, but under *Gelsemium* see DUNCAN & DEJONG, who doubted this), *Buddleja*, and *Emorya*, 870–874.]
- WAGENITZ, G. Die systematische Stellung der Rubiaceae. Ein Beitrag zum System der Sympetalen. *Bot. Jahrb.* **79**: 17–35. 1959. [Favors associating *Buddleja* with Scrophulariaceae, 19, 20.]
- . Loganiaceae. *In*: H. MELCHIOR, A. Engler's *Syllabus der Pflanzenfamilien*. ed. 12. **2**: 406–408. Berlin. 1964. [In order Gentianales, with six tribes; see MELCHIOR for Buddlejaceae.]
- WEBERLING, F. Die Bedeutung blattmorphologischer Untersuchungen für die Systematik. *Bot. Jahrb.* **77**: 458–468. 1958. [*Buddleja*, 462, fig. 3 (IV, V—leaf bases of *B. "variabilis"*); this species with "vaginale Öhrchen," which are found especially in families, including the Scrophulariaceae, that lack stipules; stresses that these should not be confused with stipules as in the Loganiaceae.]

- WHERRY, E. T., J. M. FOGG, JR., & H. A. WAHL. Atlas of the flora of Pennsylvania. xxx + 390 pp. Philadelphia. 1979. [Includes *Buddleja alternifolia*, *B. Davidii*, *Polypremum procumbens*, all introduced, 287.]
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- WUNDERLIN, R. P. Guide to the vascular plants of central Florida. i + 472 pp. Tampa and other cities. 1982. [*Gelsemium*, *Strychnos*, *Polypremum*, *Spigelia*, *Mitreola*, 294, 295.]

KEY TO THE GENERA OF LOGANIACEAE IN THE  
SOUTHEASTERN UNITED STATES

General characters: *Herbs, subshrubs, shrubs, or woody vines; stems usually with internal phloem (except Buddlejeae); leaves usually opposite, infrequently subopposite or whorled or pseudowhorled (alternate in the cultivated Buddleja alternifolia), simple and unlobed, usually with interpetiolar stipules or stipular flanges, rarely with one lobe at each side of the petiolar insertion, or stipules absent (Buddleja Lindleyana); inflorescences fundamentally cymose but otherwise diverse, lacking showy bracts; flowers actinomorphic or weakly zygomorphic, tetramerous or pentamerous; corollas tubular; stamens alternating with corolla lobes, epipetalous, uniform; anthers introrse, usually basally cleft; pollen grains usually colpate; ovary bilocular (or tetralocular in Buddleja madagascariensis); ovules many on axile or peltate-intrusive placentae; fruits capsules usually flattened contrary to the septum and dehiscent primarily septically and often loculicidally (berries in B. madagascariensis); seeds numerous; embryos straight.*

- A. Plants usually twining vines, sometimes straggling shrubs; flowers externally bright yellow, over (2-)2.5 cm long, heterostylous; stigmatic lobes 4; fruits capsules over 1.2 cm long. . . . . 4. *Gelsemium*.
- A. Plants usually herbs, subshrubs, or shrubs, rarely vines; flowers externally white, reddish, purplish, greenish, or rarely yellow (then less than 2 cm long), homostylous; stigmatic lobe(s) 1 or 2; fruits capsules less than 1 cm long or baccate.
- B. Capsules markedly cleft into 2 rounded lobes at the apex, broader than long, dehiscent to leave behind a woody, cuplike remnant; calyx lobes between  $\frac{1}{6}$  and  $\frac{1}{3}$  the length of the corolla, linear, 5; style articulated. . . . . 1. *Spigelia*.
- B. Capsules shallowly emarginate to acuminate at the apex (separating apically into 2 horns in *Mitreola*), longer than or about as long as broad, dehiscent variously without leaving a cupular remnant, or fruits baccate; calyx lobes under  $\frac{1}{6}$  or over  $\frac{1}{3}$  the length of the corolla, deltoid or ovate to rarely linear, 5 or 4; style not articulated.
- C. Plants herbaceous; flowers usually either solitary between forks in stem or in cincinni; corollas white or pink; ovaries partly inferior.
- D. Plants glabrous or with simple trichomes; leaves suborbicular to linear, over 4 mm wide; flowers in spikelike cincinni, pentamerous; capsule markedly 2-horned by apical separation of the carpels, apical lobes (horns) dehiscent adaxially only; style usually partly or completely torn lengthwise by separation of carpels. . . . . 2. *Mitreola*.
- D. Plants with multicellular broadened trichomes; leaves almost linear, under 3 mm wide; flowers mostly solitary in forks between branches with some also in cincinni or other cymose arrangements, typically tetramerous; capsule emarginate to acute apically, separating at maturity into 2 stubby apical lobes, these dehiscent adaxially and usually abaxially as well; style not torn, remaining intact on 1 apical lobe. . . . . 3. *Polypremum*.

- C. Plants usually shrubs, rarely vines; flowers in thyrsoid-paniculate arrangements; corollas usually purple, infrequently yellowish, greenish, pinkish, or white; ovaries superior.
- E. Plants unarmed; leaves penninerved; trichomes stellate and/or glandular; flowers tetramerous; fruits usually capsular (berries in *B. madagascariensis*<sup>3</sup>).  
 ..... 5. *Buddleja*.
- E. Plants armed with thorns; leaves with few arcuate lateral nerves ascending from the bases; trichomes simple; flowers pentamerous; fruits baccate. ....  
 ..... [*Strychnos spinosa*.<sup>3</sup>]

#### Tribe SPIGELIEAE Dumortier

##### 1. *Spigelia* Linnaeus, Sp. Pl. 1: 149. 1753; Gen. Pl. ed. 5. 74. 1754.

Annual or perennial herbs to subshrubs [or shrubs], sparsely to diffusely branched (often divaricately so). Stems tending to have pronounced longitudinal ridges; internal phloem present. Plants nearly glabrous or scabrous, or stems variably pubescent (mainly at nodes and along ridges), leaf blades (especially basally, along margins, and on veins), and sepals, bracteoles, and corollas slightly [to densely] pubescent also. Trichomes simple [or plants sometimes with a thick covering of "stellate hairs" composed of unicellular rays in tufts on pedestals]. Colleters present adaxially at bases of leaves, bracts, and (in some species) sepals. Leaves opposite or pseudowhorled, usually sessile or nearly so [or petiolate], the blades ovate to (mostly) lanceolate or elliptic [or suborbicular to linear], usually acuminate apically (to infrequently rounded), bases cordate to cuneate, secondary nerves often arcuate-ascending; stipules interpetiolar, membranaceous, blunt and broad to narrowly deltoid, sometimes marginally fimbriate. Inflorescences usually at ends of branches or in forks between branches, often with multiple peduncles or pedicels rising from one point, most species with spicate, branched, or unbranched cincinni, some with short monochasia, or with flowers paired or in small clusters with unequal pedicels radiating from one point, or flowers infrequently solitary; bracts and bracteoles subulate. Flowers pentamerous. Calyx lobes separate or basally connate, linear to narrowly lanceolate [to ovate] or narrowly deltoid, entire or minutely denticulate. Corollas diverse, white, purplish, reddish, or scarlet (yellow or yellow-green within in *Spigelia marilandica*), funnelform or with an elongate tube constricted at the throat, lobes shorter than the tube, valvate, usually pointed apically. Stamens included or exserted; anthers usually depositing pollen onto the pubescent subterminal shaft of the style. Ovary superior, with 2 apical lobes, each locule containing hemianatropous (*vide* Hakki) ovules inserted peltately on and partly embedded in a large, intrusive, peltate placenta inserted on the face of the septum (seen in *S. marilandica*); style much longer than ovary and stigmas, articulated above the base; stigmas unlobed or scarcely 2-lobed. Capsule strongly bilobed apically, somewhat flattened perpendicular to the septum, before dehiscence often crowned between the lobes with persistent base of style (this breaking off at articulation), both septicidal and loculicidal, circumscissile below, the segments separating from a persistent cupular

<sup>3</sup>Infrequently escaping from cultivation in Florida.



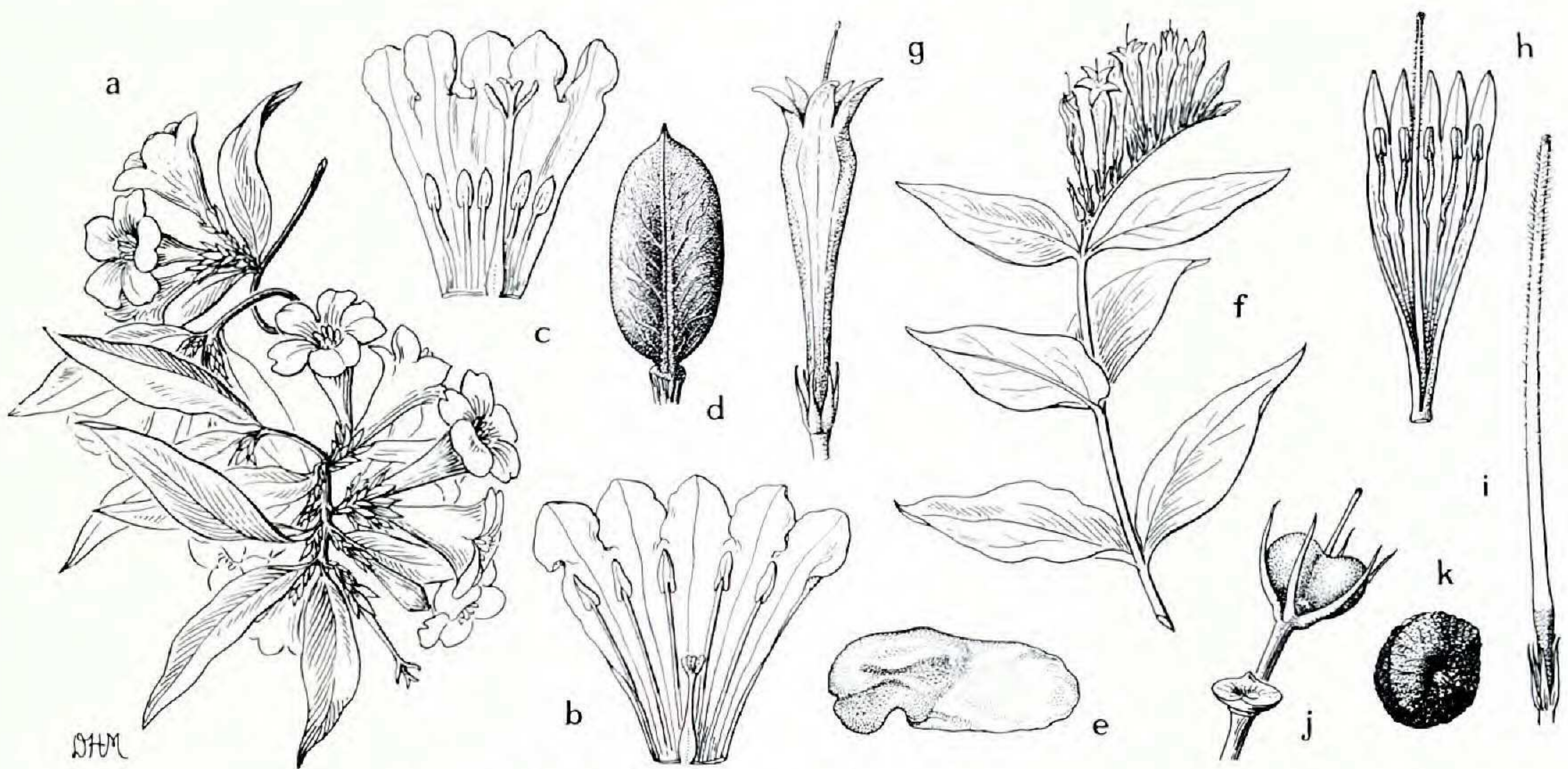


FIGURE 1. **Gelsemium and Spigelia.** a–e, *Gelsemium sempervirens*: a, flowering stem,  $\times \frac{1}{4}$ ; b, short-styled flower, opened,  $\times \frac{3}{4}$ ; c, long-styled flower, opened,  $\times \frac{3}{4}$ ; d, capsule,  $\times 1$ ; e, seed,  $\times 2$ . f–k, *Spigelia marilandica*: f, flowering branch,  $\times \frac{1}{4}$ ; g, flower,  $\times \frac{3}{4}$ ; h, corolla, opened to show stamens and style,  $\times \frac{3}{4}$ ; i, gynoecium, showing basally jointed and apically pubescent style,  $\times 1$ ; j, capsule (with persistent sepals) and persistent fruit base (sepals removed),  $\times 1$ ; k, seed,  $\times 3$ .

or boat-shaped, hardened base. Seeds verrucate or rugose, sometimes deeply pitted, usually dorsiventrally compressed, inserted peltately, angular to nearly circular (viewed from above). Endosperm initially nuclear, becoming ruminant by rapid growth into cavities formed by partial degeneration of integument.  $2n = [26], 32, 48, [64]$ . (Including *Coelostylis* Torrey & Gray ex Endl. & Fenzl.) TYPE SPECIES: *S. Anthelmia* L., the only species of the genus in the *Species Plantarum*. (Named for Paduan physician and author A. Spiegel, 1578–1625.)

Approximately 50 species distributed from the southern United States southward through Mexico, Central America, the West Indies (principally *Spigelia Anthelmia*), and South America to about the latitude of Buenos Aires, Argentina; the greatest number of species occurring in Brazil, but the genus absent or rare in the Amazon Basin. *Spigelia nicotianiflora* Chodat is disjunct between Mexico and Argentina-Paraguay (Hurley).

Earlier authorities set apart three of the six species of *Spigelia* in the southern United States as the former genus *Coelostylis*, which differs from our three other species of *Spigelia* most conspicuously in having usually white (vs. mostly reddish) flowers borne singly or in small pseudoumbellate clusters or short monochasia (vs. in spicate cincinni). One species formerly placed in *Coelostylis*, *Spigelia loganioides* (Torrey & Gray ex Endl. & Fenzl) A. DC., is a rare endemic in Levy, Marion, and Sumter counties, Florida, where it grows in low, moist, shady habitats, often calcareous hammocks, or elevations in river bottoms. Flowering takes place (April–)May through July. (For ecological details see Kral and Godfrey.) It is closely related to *S. texana* (Torrey & Gray) A. DC. *Spigelia texana* sensu stricto tends to be more branched and to have shorter corollas (usually 9.5–12 mm vs. generally over 12 mm in *S. loganioides*). It is endemic

to southern Texas in dry habitats, as well as in “swamp” and floodplain, and flowers (May–)June through August. The third species once segregated in *Coelostylis*, *S. Lindheimeri* Gray, often has a characteristic reticulation on the capsule and shorter, narrower leaves, a more compact habit (less erect and with internodes shorter than leaves), more basal branching, and smaller corollas (less than 1 cm long in Texas; to 13 mm in Mexican material) than the other species assigned to *Coelostylis*. *Spigelia Lindheimeri* inhabits relatively dry thickets and prairies in Texas and Mexico and flowers mostly from March through April in Texas—earlier than the other two species. As reflected by Hurley’s broad but unpublished concept of *S. texana* encompassing all of the elements above, these three “species” are not easily distinguished and are in need of renewed study. The literature suggests that the seed coats may provide useful characters.

Of the three remaining species, *Spigelia marilandica* (L.) L., pinkroot, Indian pink, wormgrass,  $2n = 48$ , is the most widespread in our area and is recognized by its uniquely long (mostly 3.5–5.5 cm) tubular corollas that are scarlet on the outside and yellowish within. This species ranges from South Carolina and scattered localities farther north,<sup>4</sup> southward to northern Florida and west to southern Illinois, Missouri, Oklahoma, and Texas.

*Spigelia marilandica* seems to prefer rich soil at margins of or sometimes within woods but shows appreciable ecological amplitude, with its tolerances extending to rocky places. Its blooming period is from April (toward the south) into July or even October in the Big Thicket region of Texas (*vide* Ajilvsgi). *Spigelia marilandica* appears to be pollinated by the ruby-throated hummingbird, *Archilochus colubris* (L.) (see Austin).

*Spigelia gentianoides* Chapman ex DC. is most like *S. marilandica* but has shorter (less than 3.5 cm), pale pinkish or purplish corollas and included (vs. exserted) styles. Found in Jackson County (Kral) and reported once each from Washington, Calhoun, and Liberty counties (Godfrey) and Gadsden County (Hurley), western Florida, this rare species inhabits upland *Quercus-Pinus* woods (Kral) and flowers in May and June.

Our sixth species, *Spigelia Anthelmia* L., worm grass,  $2n = 32$ , has distinctively short (less than 1 cm) corollas and a pseudowhorl of large “bracts” beneath the inflorescence. The capsules are warty (vs. smooth, lineolate, or scabrous in our other species). Its distribution stretches from South America and the West Indies to Monroe and Dade counties, Florida, where it is weedy and colonial in hammocks, in cultivated places, and along roadsides. It is

<sup>4</sup>The present northeastern limit of *Spigelia marilandica* is most likely partly attributable to commercial collecting, cultivation, and habitat destruction. *Spigelia marilandica* has been recorded from—but is now rare or absent in—Pennsylvania (see Noll, Hurley; *cf.* Muhlenberg), Maryland (one unnumbered specimen at GH is labeled “Maryland” in Asa Gray’s handwriting; see also Griffith; not listed in Boone as recently collected), Delaware (Hurley), New Jersey (Stone believed any presence to have resulted from introduction), Virginia (few reports—e.g., see Griffith; Hurley; Holm, 1892), and North Carolina (according to Youngken, once abundant; Stockberger mentioned it in 1907 as not common but present in low and middle districts of the state; the only specimen at A/GH is *Harbison s.n.*, Macon Co., North Carolina, 1899).

naturalized in Africa and in the Malay Archipelago. Leenhouts (1962) reported autogamy in this species.

Recognizing no formal infrageneric subdivisions, the De Candolles treated 33 species of *Spigelia* in the *Prodromus*. In the *Flora Brasiliensis*, Progel sorted 31 species into five sections that Solereder maintained in the first edition of *Die Natürlichen Pflanzenfamilien*. Except for Morelle and Bravo, who recognized a sixth section, modern authors, including Hurley, have ignored the sections, a practice probably best continued at least until the genus is revised again. In the meantime, new species accumulate, and the taxonomy leans heavily on regional treatments such as those of Bravo (Argentina), Smith (eastern South America), Smith and colleagues (Santa Catarina, Brazil), Guimarães & Pereira (Brazil), Macbride (Peru), Ewan (Colombia), Blackwell (Panama), Gibson (Guatemala), Alain (Cuba), and Gray (North America). An unpublished revision of *Spigelia* (1968) comprises a doctoral dissertation by Homer Hurley at George Washington University.

Distinguishing characteristics of *Spigelia* are noted in the family discussion.

The introrse anthers deposit pollen onto a pubescent section of the jointed style immediately beneath the short stigmatic lobes in most species.

Palynological data on *Spigelia* are sparse and contradictory. Observations show the grains usually to be (2-) 3- or (4-)colpate and suboblate or oblate and to have the tecta nearly psilate to shallowly undulate or verrucate and perforate, with the perforations scattered or in sunken clusters. Contradicting previous indications, Hoc & Bravo established colpus membranes as present, although easily destroyed by acetolysis. (Also see Erdtman; Punt, 1980; Punt & Leenhouts; and Melhem & Takahashi.)

“Spigeline,” reported in the literature to be an alkaloid of *Spigelia marilandica* and other species, needs confirmation by modern techniques. Bisset (1980a) maintained that “nothing is known” of the nature of alkaloids in *Spigelia*.

Solereder (1892) called attention to chlorophyll in the seeds.

The outstanding use of several species of *Spigelia* is to expel parasitic worms. *Spigelia Anthelmia* and *S. marilandica* are both said to have served North American Indians as vermifuges, and both received substantial attention for the same purpose in 18th- and 19th-century scientific-medical journals. In the United States *S. marilandica* became a popular folk cure for worms among southern settlers and rose to temporary prominence in formal medicine. Two problems plagued its use. First, commercial collectors often adulterated and confused it with different species, the contamination remaining to this day a nuisance in the ample literature on the drug. The second problem is toxicity—*S. marilandica* and *S. Anthelmia* are both blamed for killing patients (and, as related by Morton, the latter has been used to kill fish, dogs, and criminals in South America). Symptoms of overdose include delirium, vertigo, speech abnormalities, convulsions, and troubles with the eyes: pain, dilated pupils, spasms, strabismus, and dim vision. Merely touching the South American *S. pedunculata* HBK. is risky, according to García-Barriga and Ewan. It is an ingredient in some curares and is used to kill domestic animals, fish, and insects (Hurley).

*Spigelia splendens* Hooker is a minor tropical ornamental.

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## 2. *Mitreola* Linnaeus, Opera Varia, 214. 1758.

Erect [or creeping] annual [or perennial] herbs or subshrubs, unbranched or branches ascending. Plants glabrate, scabrous, or puberulent [to pilose] on vegetative and reproductive organs, especially at nodes and on leaf veins and margins. Stems with internal phloem. Leaves opposite, sessile or on short petioles, the blades nearly linear to suborbicular, occasionally slightly succulent, the lateral nerves often arcuate. Stipules small and membranaceous, interpetiolar or inserted between sessile leaves, deltoid to forming a short transverse ridge [or acuminate], infrequently taking the form of 1 lobe at each side of the foliar insertion, such lobes connected by a ridge or rarely unconnected. Inflorescences usually pedunculate, tightly condensed to uncrowded, made up of straight or curled, spicate, cincinnous branches, these in cymose arrangements (usually with multiple orders of branching, the branches often unevenly pseudumbellate or in dichasial pairs, or sometimes arising laterally from a well-defined determinate central axis). Flowers sessile or on short pedicels, pentamerous, each opposite a lanceolate to subulate bract and associated with an inconspicuous bracteole (not consistently discernible). Calyx lobes separate or basally coalescent, elliptic to ovate or deltoid, rounded to acuminate apically. Corolla white or infrequently pinkish [to violet], when dry usually with dark longitudinal veins and/or with the base purplish and the lobes creamy, urceolate, slightly exceeding to about 4 times longer than calyx, pilose in the throat, the lobes ca.  $\frac{1}{4}$ – $\frac{2}{3}$  the length of the corolla, valvate or imbricate, oblong or tapered from or just above the slightly contracted base to the rounded or acuminate apex. Stamens inserted near the base of the corolla tube; filaments about as long as or shorter than the stubby, usually cordate, dorsifixed anthers; pollen small, 3-colporate, psilate (*M. petiolata* and a few other species). Ovary partly inferior, the ovules on an expanded, stalked [or sessile?] placenta; carpels initially separate apically or separating apically, although joined at the style; style usually splitting partly or completely lengthwise by the carpellary separation or remaining intact, linear and short [or absent]; stigma knoblike. Capsule 2-horned (when style splits completely) [or capsules nearly spherical and only slightly bilobed apically]; each horn straight or bowed outward, about  $\frac{1}{3}$  to over  $\frac{3}{4}$  the length of the capsule, dehiscing longitudinally along the adaxial face (toward the other horn), often papillose, ovate or pyriform in abaxial view, rising to a usually pointed or truncate apex crowned with a half style (when this has split completely and when style is not borne intact on 1 horn) [or crowned with half stigma when style absent]. Seeds minute, reticulate, warty,

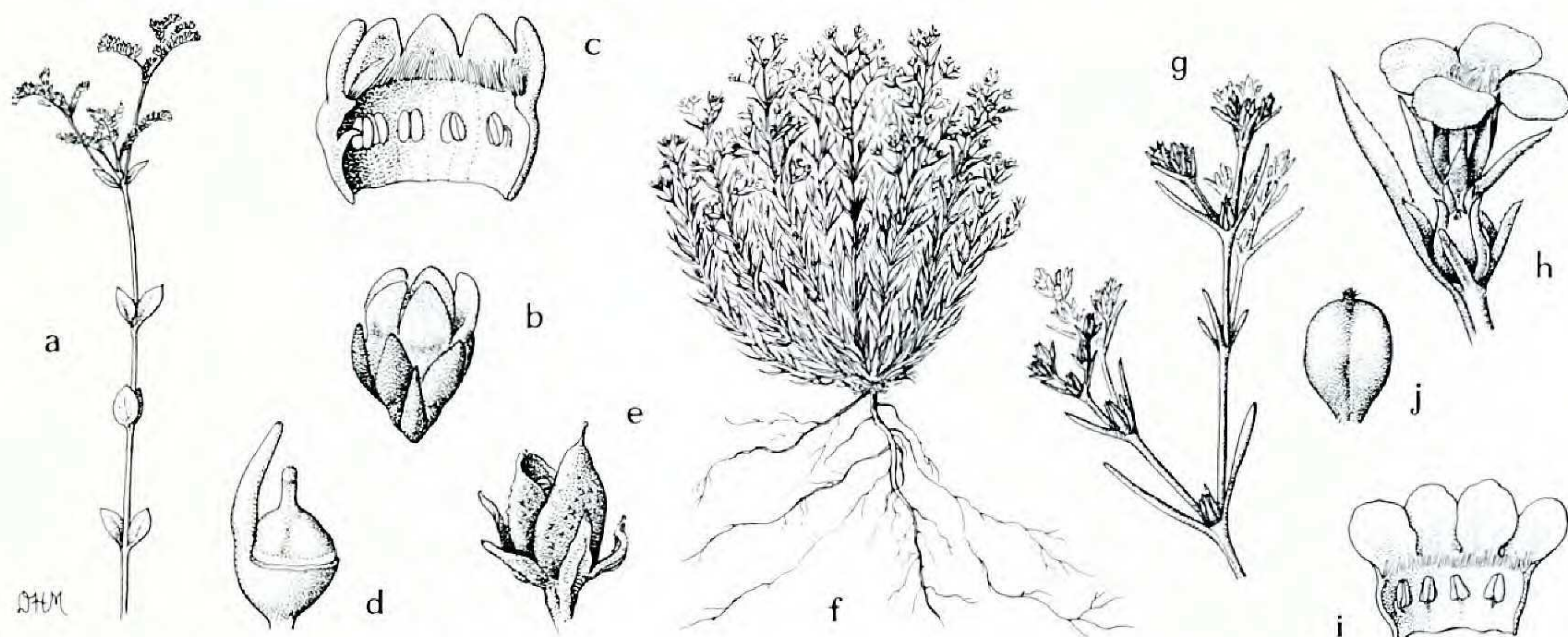


FIGURE 2. *Mitreola* (*Cynoctonum*) and *Polypremum*. a–e, *Mitreola sessilifolia*: a, habit,  $\times \frac{1}{4}$ ; b, flower,  $\times 4$ ; c, corolla, opened to show stamens and pubescent throat,  $\times 6$ ; d, gynoecium, showing intact style, all but 1 sepal removed to show point of attachment,  $\times 8$ ; e, capsule, carpels separated apically into 2 lobes, these dehisced vertically along inner (adaxial) faces (1 visible),  $\times 5$ . f–j, *Polypremum procumbens*: f, habit,  $\times \frac{1}{4}$ ; g, branch,  $\times 1$ ; h, flower and subtending leaves,  $\times 4$ ; i, corolla, opened to show stamens and pubescent throat,  $\times 3$ ; j, undehisced capsule bearing remnant of style,  $\times 5$ .

or unsculptured, attached peltately, ventrally grooved or dented, dorsally rounded, elliptic [to fusiform] in outline. Embryo nearly linear. (*Cynoctonum* J. F. Gmelin, Syst. Nat. ed. 13. 2: 306, 443. 1791, not E. H. F. Meyer, 1838.) TYPE SPECIES: *Ophiorrhiza Mitreola* L. = *Mitreola petiolata* (J. F. Gmelin)<sup>5</sup> Torrey & Gray, the only species known to Linnaeus. (Name diminutive of Latin *mitra*, miter, from the twin-peaked capsule.)—MITERWORTS, HORNPODS.

In Leeuwenberg's revision of *Mitreola*, he recognized six species: *M. pedicellata* Bentham (northern India and neighboring regions), *M. reticulata* Tirel (North Vietnam), *M. sphaerocarpa* (Leenh.) Leenh. (Borneo), *M. turgida* Jovet (Madagascar), and the two species in the United States. Li added a seventh species, *M. petiolatoides*, from Yunnan Province, China.

*Mitreola petiolata* (*Cynoctonum petiolatum* J. F. Gmelin, *C. Mitreola* (L.) Britton, *C. succulentum* R. W. Long),  $2n = 20$ , is distributed in warm parts of Australia, Asia, western Africa (see Heine), South and Central America, the West Indies, southern California, and much of the southeastern United States in an area defined by southeastern Virginia, Tennessee, southeastern Missouri,

<sup>5</sup>Gmelin cited no specimens and adopted the epithet for *Cynoctonum petiolatum* from the invalid and untypified *Anonymos petiolata* Walter. Authors have turned for a type to the Gronovius herbarium, which contains material linked to Linnaeus's different epithet for the same species (see annotations under Gronovius and Dandy, 1958). Leeuwenberg's (1972) citation of a "type" for *Mitreola petiolata* from Gronovius's herbarium might be broadly interpreted as the selection of a neotype, except that he later (1974, p. 9) stated in connection with the basionym, "Type apparently not preserved, not in the Walter herbarium in BM." Also in 1972, Tirel-Roudet evidently designated as "type" the same specimen as Leeuwenberg's "type" from the same year: "Virginie, Clayton s. n. in herb. Gronovius (BM!)."

southern Oklahoma, central and eastern Texas, and Florida. It is mainly a plant of the Coastal Plain.

In our area *Mitreola petiolata* generally prefers open or sometimes shady and usually wet habitats (but see discussion of *Cynoctonum succulentum* below). *Mitreola petiolata* occupies shores, marshes, hammocks, floodplains, ditches, pine savannas, swamps, swales, and abandoned fields. Its flowering period spans the entire year in Florida but becomes restricted to late summer or early autumn toward the north.

Long separated his new *Cynoctonum succulentum* from *Mitreola petiolata* (*C. Mitreola*) by its shorter inflorescences, shorter petioles (or virtually none), thicker leaves differing in shape, reduced branching, basal rosettes, and greater tolerance for drier locations in pine woods (although not to the exclusion of moist areas). Dismissing the materials of *C. succulentum* that he had examined as "vigorous young specimens of *M. petiolata*" (p. 19), Leeuwenberg (1974) denied it any formal status in his revision. That he came across "similar specimens" from Puerto Rico and Jamaica suggests that *C. succulentum* may not be endemic to southern Florida as Long thought.

The short-petioled, sometimes small, thickened leaves, minimal branching, and congested inflorescences of *Cynoctonum succulentum* approach the second universally recognized species in the southeastern United States: *Mitreola sessilifolia* (J. F. Gmelin) G. Don (*C. sessilifolium* J. F. Gmelin, *M. angustifolia* (Torrey & Gray) J. Nelson). *Mitreola sessilifolia* grows chiefly on the Coastal Plain from southern Virginia to eastern Texas but has been collected in New Mexico, southern Oklahoma, and the Bahamas. It is most often found in damp, open or partly open habitats, such as moist spots in pine woods, cleared land, swamps, marshes, shores, and ditches. Collectors often describe the sites as "grassy." In the southeastern United States, *M. sessilifolia* flowers from early summer (but as early as February toward its southern limit) through early autumn. Sessile or subsessile leaves, more congested inflorescences, and capsules more often abaxially verrucose differentiate it from *M. petiolata*. However, the boundary is sufficiently blurred for both Leeuwenberg (1974, stressing seed coats) and Long to have acknowledged the plausibility of hybridization or "introgression." I find certain specimens difficult to place in one species or the other.

Mentioning ecological differences, Long (see also Long & Lakela) established *Cynoctonum sessilifolium* var. *microphyllum* for specimens with short (mostly under 1.5 cm vs. over 2 cm), comparatively narrow leaves having acute (vs. obtuse) apices, simple stems, and inflorescences bearing few, short branches. The distribution of this putative variety nearly matches that of var. *sessilifolia*. To back up his refusal to recognize it, Leeuwenberg (1974) cited continuity of variation in leaf size and remarked on the great differences in this character within the type collection of *Mitreola sessilifolia*. The pattern of variation in sizes and shapes of leaves on specimens in the Harvard Herbaria (A and GH) does indeed weaken the concept of var. *microphyllum*.

Torrey & Gray assigned specimens having narrowly elongate and "closely sessile, obscurely veined" leaves to *Mitreola sessilifolia* var. *angustifolia* (*Cynoctonum angustifolium* (Torrey & Gray) Small, *M. angustifolia* (Torrey &



Gray) J. Nelson), which grows in Florida and on the Coastal Plain of Georgia. Specimens of this possible variety in the Harvard Herbaria have stipular flanges with edges either straight and horizontal or notched at the middle, whereas in other possible varieties the edges usually rise at the middle. Moreover, the abaxial lateral nerves of leaf blades of var. *angustifolia* are usually sunken or less prominent than in the rest of the species. As might be surmised by its occasional elevation to a species, var. *angustifolia* is more distinctive than var. *microphyllum* (*microphylla*), but Leeuwenberg (1974) thought it insufficiently distinct for recognition.

*Mitreola petiolata* forms vanillic and  $\rho$ -coumaric acids, according to Daniel & Sabnis.

*Mitreola* is economically inconsequential. Roots from *M. petiolata* have served in folk treatments for snake bites and worms.

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### 3. *Polypremum* Linnaeus, *Sp. Pl.* **1**: 111. 1753; *Gen. Pl.* ed. 5. 50. 1754.

Procumbent to ascending, matted to scoparioid, perennial or reportedly sometimes annual, taprooted, heliophilous herbs. Plants made up of 1 (infrequently) to innumerable (frequently) vegetative and fertile stems arising as a result of often highly congested basal branching; branching lateral (particularly toward the base of the plant) and usually pseudodichotomous-dichasial (especially distally on the plant). Tufts of short vegetative stems and associated foliage often forming dense overwintering rosettes. Plants usually scabrous-serrulate along leaf margins and frequently so on stem ridges, midribs of leaves, and sepals, also with minute, sunken hairs made up of a basal cell, a stalk cell, and usually 4 (but occasionally 8) cells comprising a broadened cap. Branchlets fluted, often with 4 sharp flanges and 2 or 4 rounded ridges, containing palisade tissue and lacking internal phloem. Leaves opposite, sessile, joined basally by a transverse membrane, the blades virtually linear, gradually tapered to acuminate apices, usually widest near or somewhat above the middle, sometimes

broadening gradually toward the base, the midribs usually prominent abaxially, other vasculature inconspicuous, containing palisade tissue on both sides. Flowers borne singly between pseudodichotomous branches, also clustered in various cymose arrangements, these usually dichasial and occasionally with cinnoid or scorpioid branches, or infrequently the entire inflorescence variously monochasial. Flowers tetramerous or infrequently pentamerous, very rarely with 6 calyx lobes, subtended by a reduced pair of foliage leaves ("bracteoles"). Calyx lobes connate basally, lanceolate, with hyaline margins, the attenuate apices continuing the thickened and abaxially keeled midribs. Corolla white, shorter than to exceeding the calyx, cruciform-salverform, with a ring of hairs in the throat, the spreading, subequal lobes oblong to obovate, rounded to truncate apically,  $\frac{1}{3}$ – $\frac{2}{3}$  the length of the corolla, imbricate. Filaments approximately as long as anthers, these cleft at both ends, dorsifixed, broadest near base; pollen grains oblate-spheroidal, tricolporate, the tectum psilate-perforate. Ovary partly inferior, flask shaped (including the style), compressed perpendicular to the septum, the ovules amphitropous (inserted transversely at middle of funiculus) or (*vide* Hakki) anatropous, on a narrowly oblong placenta inserted near the base of the septum; style very short; stigma capitate, unlobed or nearly so, papillose, about as long as style. Capsule nested in the persistent calyx, small (ca. 2 mm long), compressed, obovate to ovate, usually elliptic, septum forming a sunken vertical line, emarginate to acute at apex, there separating septicidally into 2 adaxially and longitudinally opening lobes, also usually opening along abaxial sutures, the stubby remnant of style remaining intact on 1 lobe. Seeds translucent yellow when dry, minute, irregularly polygonal, roughly isodiametric, not sculptured or faintly reticulate-rugulose. Endosperm initially cellular. Embryo stocky, the thickened cotyledons about  $\frac{1}{3}$  its length. (*Hasslerella* Chodat.) TYPE SPECIES: *Polyprenum procumbens* L. (Name from Greek *polys*, many, and *premon*, stem.)

A genus of a single weedy species distributed in South America (there nearly restricted to the north), Central America, Mexico, the West Indies, and the United States. While the northern limit probably fluctuates, most natural populations in the United States fall within the area defined by the Florida Keys, the eastern two-thirds of Texas, Oklahoma, southeastern Missouri (and collected once in the northeastern corner of this state), Tennessee, and North Carolina. *Polyprenum* has been collected but is now rare or perhaps absent in southwestern Kentucky (V. Bates, pers. comm.), southern Illinois (Mohlenbrock), and southeastern Indiana (Collins). Its range extends along the Atlantic coast to Delaware and Maryland, with a few scattered collections from farther north: southeastern Pennsylvania (in Wherry *et al.* as introduced) and adjacent New Jersey (Camden, C. F. Parker, 9-21-1865, GH, "in ballast sand"). Miller encountered *Polyprenum* on Long Island, New York.

Chodat's genus *Hasslerella*, a synonym of *Polyprenum*, is based on a disjunct population in Paraguay (see Pennell). An old report of *Polyprenum* in Chile is probably erroneous. Outpost populations in Hawaii, Guam, Wallis (near Samoa), and Palau (localities from Fosberg and Fosberg & Falanruw; specimens at US!) probably originated from recent introductions. Others certainly must exist.

*Polypreum* inhabits wet or more often dry, usually open localities at both low and high altitudes, mainly on sandy soil or even on bare sand. Favored habitats include *Pinus* savannas, other open woods, artificially disturbed places, shores, edges of swamps or woods, ditches, marshes, prairies, and littoral dunes.

*Polypreum* flowers mostly from late spring through early autumn in our area, but dates on flowering specimens from Florida cover nearly the entire year.

Three embryological attributes of *Polypreum* struck Moore (1948) as peculiar: the megagametophyte invades the micropylar canal to the ovular surface; the zygote moves from a point of origin in the micropyle to the center of the endosperm; and short, cylindrical, possibly haustorial "necks" protrude from both ends of the endosperm. In addition, the inner wall of the inner epidermis (an endothelium) thickens in the seed coat.

Moore (1947, 1948) counted  $2n = 22$  and  $3n = 33$  using roots and endosperm from *Polypreum procumbens* collected in North Carolina. His use of sectioned material makes verification desirable. The data on one herbarium specimen from Guyana (*K. R. Robertson & D. F. Austin 269*, 1967 (GH)) give  $2n = 20$ . Moore's illustrations show heterogeneous chromosomes intergrading in length.

The relationships of the genus are discussed under the family treatment.

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#### Tribe GELSEMIEAE G. Don

#### 4. *Gelsemium* A. L. de Jussieu, Gen. Pl. 150. 1789.

Woody, twining, climbing or sometimes creeping, perennial vines (individuals of *Gelsemium sempervirens* with leafless runners when traversing areas of bare rock), or occasionally shrubby. Adventitious roots forming on rhizomes. Stems with internal phloem (seen in *G. sempervirens*). Plants glabrous or puberulent-hispidulous on axes (particularly at nodes), petioles, basal portions of foliar midribs, and (in *G. Rankinii*) often mid-basal portions of abaxial leaf blades. Leaves opposite or whorled, petiolate, the blades mostly narrowly lanceolate to elliptic or ovate, rarely linear, usually acuminate apically, cuneate to truncate basally. Petiole bases usually connected by a stipular flange, with colleters axillary and between petioles. Flowers solitary on pedicels in leaf axils or in axillary or terminal pairs or clusters often composed of a short, bracteate, determinate central axis bearing pedicellate flowers or branch axes, sometimes multiple pedicels or peduncles arising in 1 axil. [In *G. elegans* inflorescences large compound cymes usually with well-developed central axes.] Pedicels bearing 1 to many deltoid to ovate or lanceolate, often ciliate bracteoles, frequently associated with colleters. Flowers showy, pentamerous, heterostylous [or homostylous], fragrant or not. Sepals separate, oblong-elliptic to ovate or deltoid, rounded to acuminate apically, often ciliate, caducous or persistent. Corolla yellow or orange [sometimes with red markings in *G. elegans*], funnelform, actinomorphic to slightly zygomorphic, lobes imbricate, mostly  $\frac{1}{5}$ – $\frac{1}{2}$  the length of the tube, rounded to obtuse [to acuminate] and sometimes apiculate or emarginate apically. Stamens inserted at base of corolla tube; anthers connivent or separate, sagittate; pollen grains usually nearly spherical to prolate, tricolporate, the endoapertures with distinct margins and 2 lateral extensions, tectum striato-reticulate (based on Punt, 1980). Ovary bottle shaped, gradually tapered to style, containing anatropous ovules (*G. sempervirens*) on axile placentae; stigmas twice forked into 4 papillate lobes. Capsule flattened perpendicular to septum, septicidal and loculicidal, splitting partly or completely into 4 segments, elliptic or oblong in outline, beaked with persistent style base [or beak absent]. Seeds flat, irregular in outline, with a thin, tawny wing at 1 end (*G. sempervirens*) or wing absent (*G. Rankinii*) [or seeds surrounded by an erose wing in *G. elegans*]; embryo nearly cylindrical but slightly spatulate (*G. sempervirens*). TYPE SPECIES: *Bignonia sempervirens* L. (= *Gelsemium sempervirens* (L.) Jaume St.-Hil.) (Generic name dating back at least into the seventeenth century; Italian, Medieval Latin, and archaic English words for jasmine are similar to *Gelsemium*; name ultimately probably from Arabic or Persian *yasmin* or similar words for jasmine (*Jasminum*, Oleaceae) possibly combined with Italian *gêlso*, for species of *Morus*.)

A genus of three species distributed in southeastern North America, Central America, and Asia. (See Ornduff, who revised *Gelsemium* and studied its reproductive biology.)

*Gelsemium sempervirens*, Carolina jasmine, yellow jessamine, or yellow jasmine, ranges from southeastern Virginia southward to (mostly northern) Florida and westward to Tennessee, Arkansas, eastern Texas, and perhaps (as in Vines but not other sources) Oklahoma. Disjunct populations occur in southern Mexico and Guatemala. Its ecological tolerances are broad—reported habitats include dry, sandy soil, savannas, pine barrens, rock outcrops, thickets, hardwood forests, hammocks, edges of salt marshes, dune hollows, boggy areas, shady creek bottoms, and swamps. Godfrey & Wooten (p. 516) mention “lowland woods where water stands only for short periods.” In our area *G. sempervirens* blooms mostly from (January or) February through April (or early May toward the north) and infrequently in autumn (or rarely at other times). Most seeds are dormant for two years (Speer).

Beyond ecological and phenological differences, the second species in our area, *Gelsemium Rankinii* Small,<sup>6</sup> differs from *G. sempervirens* in its acuminate, persistent, nonciliate sepals (vs. sepals less sharply pointed to rounded, deciduous, and usually ciliate); pedicels with few, nonciliate bracteoles (vs. pedicels covered with ciliate bracteoles); wingless seeds (vs. seeds winged at one end); usually scentless flowers; and more pubescent petioles. Hybridization between *G. Rankinii* and *G. sempervirens* is strongly inhibited (Ornduff, 1970), which is not surprising since they grow close together in some places (occasionally leading to mixed collections).

*Gelsemium Rankinii* is nearly totally confined to wet habitats on the Coastal Plain from North Carolina to eastern Louisiana, except for southern Florida. It flowers slightly later than the preceding species, mostly in March and April, although as early as January toward its southern limit, and infrequently in September and October.

The Asian *Gelsemium elegans* (Gard. & Champ.) Benth ( *Leptopteris sumatrana* Blume) differs from the American species in its large, elaborate inflorescences (vs. flowers solitary or in small clusters), its smaller flowers tending to have pointed (vs. rounded) corolla lobes, its less flattened capsules, and its

<sup>6</sup>From the three herbarium sheets that bear specimens of *Gelsemium* in Michaux's herbarium, Ornduff (1970) accepted as the holotype of *G. nitidum* Michaux (Fl. Bor. Am. 1: 120. 1803) the only one evidently thus labeled by Michaux. Holotype status for this specimen is debatable, however. “A holotype is the one specimen or other element used by the author or designated by him as the nomenclatural type” (ICBN, Art. 7.3). Michaux cited no specimens when *G. nitidum* was published, and he appears to have used materials other than the alleged holotype, since the floral details in his description are unlikely to have come from this evidently fruiting specimen. (Seen only on fiche 29 of IDC micro-edition; buds or damaged flowers may be present.) Several flowers in good condition are on one of the two other herbarium sheets. A second problem is that the sheet in question appears to consist of a mixture of *G. sempervirens* and *G. Rankinii*. If so, the use of this specimen for a lectotype requires choosing the material (species) on it that corresponds best with the original description of *G. nitidum*, which could threaten the more recent name *G. Rankinii*. Recognizing the ambiguities, Ornduff suggested dismissing *G. nitidum* as a *nomen confusum* to be placed in the synonymy of *G. sempervirens* because of Michaux's characterization of floral scent in the protologue of *G. nitidum*. (However, floral scent is not unknown in *G. Rankinii*—see Duncan & Dejong.)

seed surrounded by a wing. It grows in southern China, Burma, Thailand, Laos, Vietnam, India (Assam), Borneo, and Sumatra.

Gelsemiums are recognized as trailing or climbing vines or straggling shrubs with large, showy, yellowish, infundibular, heterostylous (ours), often fragrant flowers with sagittate anthers and four-parted styles. The seeds are flat, and they are winged in two of the species. The capsules are compressed perpendicularly to their septa.

Most modern authors pair *Gelsemium* with *Mostuea* Didr. as (or in) the tribe Gelsemieae. Both *Gelsemium* and *Mostuea* have heterostylous flowers (except races of *G. elegans*), four stigma lobes, and similar indole alkaloids (sempervirine and probably gelsemine are shared) and pollen. *Gelsemium* differs from *Mostuea* in its chromosome number ( $2n = 16$ , vs. 20), nonvestured pits in the vessel elements, oblong-elliptic (vs. usually bilobed) capsules containing many (vs. one or two) seeds per locule, and yellow or partly red (vs. usually mostly white) corollas. (See Ornduff, 1970; Bisset *et al.*; Punt, 1980; Leeuwenberg & Leenhouts; Mennega; and Saxton.)

*Gelsemium sempervirens* is unusual anatomically in that a cambium and secondary xylem form between the intraxylary phloem and the primary xylem (Solereider, 1908).

Aspects of the breeding system of *Gelsemium* elucidated by Ornduff (1970, 1979, 1980) include its pollination mostly by large-bodied bees (although small bees visit *G. sempervirens*) and its heterostyly that is associated with a self-incompatibility system within each morph in both American species.<sup>7</sup> Ornduff also showed that some races of *G. elegans* are homostylous, while others are heterostylous; that in *G. sempervirens* pin flowers are homozygous recessives at one locus, thrums heterozygous; and that in *G. sempervirens* intrafloral pollen transfer is appreciable. Corollas of *G. sempervirens* show pronounced ultraviolet patterns with light lobes (reflecting) and dark tubes (absorbing) (see photos in Eisner *et al.*).

*Gelsemium sempervirens* is a favorite, often-cultivated, wild flower in the southeastern United States and is the state flower of South Carolina. Highly bioactive, it was once prominently used as folk and formal remedies, which in overdoses no doubt killed more patients than it saved. (Medicinal applications of *Gelsemium* are discussed in Holm, Holmes, Lloyd, and Speer.) It remains a peril to livestock and to children who suck nectar from or eat the flowers (see Morton, Blaw *et al.*). The nectar is reputedly poisonous to young bees (Gowanloch & Brown) and may have been the source of the toxin in honey that killed three people in South Carolina (as related by Chesnut, who remained skeptical that *Gelsemium* was at fault). Also used medicinally and said to poison visiting insects, *G. elegans* has been an instrument of murder, execution, and suicide in Asia (Bell, Chesnut, Ford *et al.*). When eaten, *Gelsemium* inhibits synaptic activity of motor neurons (Perkins & Payne). Symptoms include weakness and paralysis, drooping of the jaw, staggering, ptosis, visual disturbances, slurred speech (or inability to speak), dilated pupils, feeble (or abnormal) heart-

<sup>7</sup>Heterostyly may be principally an adaptation that minimizes inappropriate pollen deposition in plants already having incompatibility systems (see Proctor & Yeo).

beat, convulsions, and (in certain cases death by) respiratory paralysis. (Consult Chesnut, Blaw *et al.*, Hardin, Holmes, and Perkins & Payne for details.) *Gelsemium sempervirens* also causes dermatitis (McCord).

Indole alkaloids are responsible for the toxicity of these plants. *Gelsemium sempervirens* contains sempervirine, yohimbine and/or derivatives (Neuss), gelsemine, gelsemicine (the principal poison), gelsedine, and gelsevirine (sometimes spelled "gelseverine"). Similar alkaloids, including sempervirine, gelsedine, gelsevirine, and gelsemine, have been isolated from *G. elegans*. Because the literature on alkaloids in *Gelsemium* is extensive, beset with nomenclatural confusion, and chemically complex, Saxton's monographic review is especially helpful. (Also see Bindra; Bisset, 1980a; Cueilleron *et al.*; Jin & Xu; Kusakürek *et al.*; and Yang & Chen, 1982a, 1982b, 1983.)

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Tribe BUDDLEJEAЕ Bentham<sup>8</sup>

5. **Buddleja** Linnaeus, Sp. Pl. 1: 112. 1753; Gen. Pl. ed. 5. 51. 1754.

Sarmentose subshrubs, climbers (*Buddleja madagascariensis*), or usually shrubs [or herbs or trees]. Plants with stellate and sometimes candelabrum-shaped trichomes with 4 or more rays per whorl, the trichomes frequently forming a felt on the abaxial side of leaf blades (these rarely glabrate), petioles, and young axes, very dense to absent on adaxial leaf surface and calyx, and absent to felted externally on corolla. Calyx and corolla with dense to sparse or absent, amber to white, often glistening (when dry), glandular hairs externally with 2-or-more-celled swollen heads on short stalks, such hairs sparse or absent on vegetative organs. Twigs angled or terete, internal phloem absent. Leaves petiolate [or sessile, sometimes perfoliate], opposite or subopposite [rarely alternate], ovate, lanceolate or elliptic, often quite narrow [or linear and extremely short], acuminate to long-attenuate at the apex, the base subcordate to more often cuneate or caudate, margins entire, sinuate, crenate, or serrate [or lobed]; stipules interpetiolar, thick and green (when living), blunt, or absent. Inflorescences terminal or infrequently lateral, usually cylindrical or narrowly conical thyrses (but the long main axis at least sometimes determinate), the lateral units infrequently single flowers, more often simple or compound, sometimes congested and fasciculate dichasia [or arranged into spherical heads or series of pseudovercils in some species], branch axes resembling the primary axis in specimens of *B. madagascariensis*; flowering branches smaller than the main inflorescence, commonly arising from upper leaf axils; basal bracts intergrading with foliage leaves or sharply reduced, distal bracts and bracteoles linear or narrowly deltoid. Flowers sessile or on short pedicels, actinomorphic or nearly so, tetramerous [very rarely pentamerous], perfect or with anthers or gynoecium sterile, sterile organs resembling the functional organs or reduced. Calyx tubular, cylindrical or flared or urceolate, frequently about as long as the corolla lobes, topped with deltoid teeth less than  $\frac{1}{10}$ – $\frac{1}{3}$  (to ca.  $\frac{1}{2}$ ) the length of the calyx. Corolla usually purplish (*B. Lindleyana*, *B. Davidii*, often with an orange center in the latter, some cultivars of this with white, pinkish, or nearly red corollas) or yellowish or pale orange (*B. madagascariensis*), salverform or infundibular, sometimes curved, with a long, narrow, cylindrical or slightly flared tube [or the tube hemispheric], pubescent within (only at the base in *B. madagascariensis*), the lobes less than  $\frac{1}{10}$ – $\frac{1}{3}$  (or ca.  $\frac{1}{2}$ ) [or exceeding] the length

<sup>8</sup>Although cited by some authors as the authority for this tribal name, Bartling published *Buddlejea* as a subgroup of undesignated rank under ordo Scrophularinae in his *Ordines Naturales Plantarum* (1830). Bentham published *Buddlejeae* as a tribe on June 1, 1835, according to a statement printed at the base of an associated plate (*Bot. Regist. pl. 1770*). If June 1 is correct, Bentham's publication antedates David Don's tribe *Buddlejeae* in the July issue (vol. 19, p. 111) of the *Edinburgh New Philosophical Journal* of the same year.

of the tube, erect or spreading, obovate to ovate, frequently elliptic-oblong, sometimes broader than long, rounded or truncate apically, imbricate [or valvate], the margins entire or crenate-erose. Stamens inserted below middle of corolla tube to near the mouth; anthers included [or exerted], dorsifixed, cleft at the base, oblong or broadened basally [to almost orbicular], longer than the filaments [except in sect. *CHILIANTHUS*]; pollen variable, 3- or 4- [or 8-]colporate, the exine smooth, punctate [or reticulate]. Ovary superior, with 2 or 4 (*B. madagascariensis*) locules, nearly cylindrical or turbinate and somewhat compressed (or almost spherical in *B. madagascariensis*), containing anatropous or hemianatropous ovules on elongate axile [or partly parietal] placentae (these attached at the apex of the septum in *B. Davidii*); style about as long as ovary (or much longer in *B. madagascariensis*), included [or exerted]; stigma elongate and narrow to globose. Fruits fusiform to ovoid, primarily septicidal but also apically loculicidal capsules (*B. Davidii*, *B. Lindleyana*) or berries (*B. madagascariensis* and others of sect. *NICODEMIA*), surrounded by the persistent calyx. Seeds minute, fusiform-linear (*B. Davidii*) or polygonal, with or without a narrow, irregular wing (*B. Lindleyana*), or unwinged and ovoid to ellipsoid (*B. madagascariensis*). Endosperm initially cellular. (Including *Adenoplea* Radlk., *Nicodemia* Ten., and *Chilianthus* Burchell.) TYPE SPECIES: *B. americana* L., the only member of the genus in the *Species Plantarum*. (Named for British clergyman and botanist Adam Buddle, ca. 1660–1715.)—BUTTERFLY BUSH.

A genus of some 100 species (Norman, pers. comm.) in tropical and subtropical (and, to a limited extent, warm-temperate) Asia, the Arabian Peninsula, eastern and southern Africa, Madagascar, the Mascarene Islands, and America. Centers of diversity are in and about south-central China, including the eastern Himalayas, and tropical America. Roughly one-third of the species occur in the Old World. The widespread *Buddleja asiatica* Lour. occurs across most of southern Asia, and the range of *B. americana* reaches from northern Mexico to the West Indies and Bolivia. Fifteen species are indigenous to Mexico, and five to the southwestern United States. Of the handful of alien species cultivated in this country, three persist or spread from plantings in the range of the Generic Flora.

Section *NEEMDA* Bentham is represented in the southeastern United States by *Buddleja Davidii* Franchet,  $2n = 76$ , and *B. Lindleyana* Fortune,  $2n = 38$ . The former, the best-known species of the genus, is indigenous to China and possibly Japan. Being hardy and popular in gardens, it turns up adventively in scattered regions, such as much of Europe, where it colonized rubble left after the Second World War. The spotty distribution of *B. Davidii* in the United States includes mostly, but not exclusively, the states along the mid-Atlantic seaboard. It may be encountered in our area on disturbed ground, along roadsides, on shores, and in rocky places. Norman (pers. comm.) adds that it readily escapes from cultivation around Seattle, Washington. The natural polymorphism of *B. Davidii* has been the source of an array of cultivars. Usually purplish to sometimes white, pinkish, or nearly red, fragrant flowers typically with straight corollas having orange in the throats allow quick recognition of this species.

Our other member of sect. NEEMDA, *Buddleja Lindleyana*, is cultivated and naturalized beyond its homeland in China and nearby parts of eastern Asia. Although less hardy than the preceding species, *B. Lindleyana* seems to be better established in our area. It is present in and out of cultivation in probably all of the Southeastern States and Texas, being most clearly "naturalized" from North Carolina to southern Florida. Escaped populations arise on disturbed ground, roadsides, and shores and in pine woods. This species differs most saliently from *B. Davidii* in having longer, curved corolla tubes more abundantly provided with glandular hairs, usually simple lateral dichasia, leaf margins entire to irregularly crenate or dentate, or infrequently unevenly serrate (vs. generally distinctly serrate), no stipules (ephemeral in *B. Davidii*), and polygonal (vs. linear-fusiform) seeds.

Sect. NICODEMIA (Ten.) Leeuw. is represented by *Buddleja madagascariensis* Lam.,  $2n = 38$ , an attractive garden species from Madagascar that escapes to disturbed sites in central-western peninsular Florida. Its yellowish or somewhat orange corollas with the stamens inserted high in the tube (vs. near or below the middle), tetralocular (vs. bilocular) ovaries, and berries (vs. capsules) are unique among our species. (I have not seen fruiting material from the United States.) Dried specimens are densely brownish-tawny pubescent. *Buddleja madagascariensis* flowers in the Southeast during winter, as opposed to the summer or autumn blooming of the two other species.

The foremost taxonomic treatments of *Buddleja* have been by Bentham (1846, the entire genus), Marquand (species in the Old World), Leeuwenberg (1979, African and Asian species), Norman (1967, 1982, species from North America and Ecuador), and Norman & Smith (in Smith *et al.*, 1976, species from Santa Catarina, Brazil). Divergent views complicate the infrageneric taxonomy. Bentham recognized two sections subdivided into components of unstated rank; Marquand rejected Bentham's arrangement and set up four "convenient" series for species in the Old World. In 1979 Leeuwenberg explained in effect that Marquand's series depend on few or single and feeble characters and consequently incorporated them all in his large, emended, and not subdivided section NEEMDA. Leeuwenberg correctly changed the name of Bentham's sect. *Lozada* to sect. BUDDLEJA, restricting it to three American species.

Leeuwenberg's two other sections are based on former genera from the Old World. The three species of sect. CHILIANTHUS (Burchell) Leeuw. stand out in *Buddleja* because their stamens are exerted on long filaments from broad and shallow corolla tubes. Chromosomal morphology and number help bind this section to the rest of the genus. Members of Leeuwenberg's sect. NICODEMIA have berries, rather than the capsules that are more typical of other species of the genus. The merger of *Nicodemia* with *Buddleja* into one genus is supported by hybridization, anatomy, limited chemical data, chromosomal morphology, and chromosome numbers (Leenhouts, 1962; Moore, 1947, 1960).

Norman will revise the infrageneric taxonomy in her upcoming treatment of the South American species.

*Buddleja* is probably most closely related to *Emorya*, from the New World, and *Nuxia*, from the Old, according to Leeuwenberg (1979) and Norman (1967). In contrast with *Buddleja*, *Emorya* has leaves with sinuate margins (unusual

in *Buddleja*), stamens exerted on long filaments from long corolla tubes (vs. on short filaments from long corolla tubes and usually included, or exerted on long filaments from short corolla tubes), styles protruding beyond the anthers, and a glabrous annular disk at the base of the ovary. Attempted crosses between *Emorya* and *Buddleja* have so far failed, despite the near morphological identity of their chromosomes.

*Nuxia* has relatively short corolla tubes bearing exerted stamens on filaments longer than those in most species of *Buddleja*. Section CHILIANTHUS has been included in and approaches *Nuxia* in having similar flowers and pollen (Punt, 1980; Punt & Leenhouts) and in the distribution of iridoids (Hegnauer & Kooiman). *Nuxia* is distinguished from sect. CHILIANTHUS and from the rest of *Buddleja*, however, by apically confluent (vs. separate) anther cells.

*Nuxia*, *Emorya*, and *Buddleja* sensu lato have the base chromosome number 19 in common.

Norman (1967, 1982), Ariza Espinar, and Norman & Smith (in Smith *et al.*) showed over thirty American species to be dioecious, usually fairly obscurely so. Staminate and carpellate flowers were similar externally or infrequently differed in size and/or shape; young sterile ovaries were either stunted or similar to fertile ones; and infertile anthers were reduced. Ariza Espinar told of conspecific staminate and carpellate buddlejas being described as separate species. Norman (1982) discovered *Buddleja Jamesonii* Benth and *B. americana* to be trioecious (perfect, carpellate, and staminate flowers in different collections). One otherwise staminate plant of *B. racemosa* Torrey bore a few seeds, and carpellate plants of the same species in cultivation formed a small number of viable seeds, seemingly without pollination. This may have been due either to apomixis or to incompletely sterile anthers (Norman, 1967). If Ariza Espinar's suspicions are borne out, three species in Argentina have functionally perfect flowers, and Norman (pers. comm.) reports perfect flowers in at least the South American *B. tubiflora* Benth and *B. australis* Vell.

Species from the Old World are less well studied in this regard. In *Buddleja Davidii* and *B. Lindleyana* only a portion of the flowers set fruit, frequently with inflorescences devoted completely or nearly so to either flowers that set fruit or presumably staminate ones that wither without forming capsules. (In 1984 almost all of the flowers of an individual of *B. Davidii* collected wild and grown in the Arnold Arboretum produced fruits. The pollen probably came from several nearby members of the same species.) Moore (1967) related the production of viable vs. nonviable pollen in the Asian species *B. crispa* Benth cultivated in Canada to the season (i.e., under photoperiodic control?).

Certain species of *Buddleja* are self-compatible; others (including *B. Davidii*) are self-incompatible or nearly so (Keenan, 1969a; Moore, 1949, 1952).

Buddlejas usually grow completely in the open, or in scrubby woods or at their edges, and they commonly occur in disturbed or rocky places, at high elevations, on bluffs or steep slopes, and in dry (to wet) soil. *Buddleja Davidii* and other species tolerate high concentrations of calcium.

Flowers of *Buddleja Davidii* are sufficiently alluring to butterflies and other insects to serve as popular study sites for lepidopterists and as textbook examples of flowers visited by butterflies.

Diploid ( $2n = 38$ ) species of *Buddleja* grow in Asia, Africa, and America. Numerous tetraploids are present in Asia and America, and probably also on Madagascar and nearby islands. One hexaploid is known from the New World (Norman, pers. comm.), while in Asia there are several hexaploids, as well as two known 12-ploids and one mixed 8-, 16-, and 24-ploid species.

Among species from the Old World cultivated in Ottawa, Canada, Moore (1961) found most polyploids to be long-day plants (or to flower late in the season by virtue of requiring a preliminary period of growth) and to have spicate inflorescences. He interpreted both features as evolutionary advancements over the short-day requirement and the often shorter, leafier, and otherwise presumably less-specialized inflorescences of most diploid species. (Norman, 1967, disagreed about evolutionary trends in the inflorescences.) Moore (1961) supposed multiple diploid species to have been ancestral to the Asian polyploids, which he held to have "spread little beyond the point of origin" (p. 278). They are clustered in the Asian area of high species concentration mentioned above (see also Janaki Ammal). Their mutual inclination toward the long-day photoperiod notwithstanding, the polyploids are not the northernmost species.

As envisioned by Moore (1961), the relatively primitive diploid buddlejas crossed the formerly narrower Atlantic Ocean to the New World under equatorial short-day conditions and radiated northward secondarily. This accords with Norman's (1967) hypothesis that the North American species arose from South American ancestors, since the former are most similar to and have morphological "prototypes" among those in South America. (For the opposite view that *Buddleja* spread from North to South America, see Raven & Axelrod.)

In 1967 Moore observed that the New and Old World buddlejas "differ greatly," and he (1960) was unable to cross members of one group with those of the other. (At least two New World–Old World hybrids have been reported; one of these is probably a backcross involving gametes differing in chromosome number.) Moore and other authors have hybridized even morphologically dissimilar Old World species, and apparent hybridization among American species occurs repeatedly (see comments under individual species in Norman, 1967, 1982). All three of our introduced species are thought to be parents of various hybrids. Artificial crosses in *Buddleja* range in outcome from reduced fertility to early developmental failure of the  $F_1$  hybrids.

Species of *Buddleja* are most important to humans as ornamentals and as medicinal plants. All three species in our area were certainly introduced for their decorative value, which they share with several other species, as well as with various hybrids and cultivars. Applications in folk medicine counter a wide variety of ills in both hemispheres. Houghton (see also Bisset, 1980a, 1980b) compiled a survey of medicinal uses focused on eight species and attempted to relate attributed benefits to chemical constituents: remedies for the skin and eyes possibly relate to flavonoids, aucubin (an iridoid), and saponins; respiratory treatments may be based on terpenes or saponins; antiseptic qualities could be related to the aglycone from aucubin; diuresis might result from aucubin or flavonoids; and sedative and analgesic properties are possibly due to alkaloids, although scattered reports of alkaloids in *Buddleja* remain

inadequately substantiated and have in some cases been contradicted. In an earlier study Houghton isolated lignans from *B. Davidii*, and in 1984 he cited other literature documenting lignans as antihepatotoxics. Singh and colleagues looked into hypotensive activity from *B. asiatica*. Some, if not all, species are poisonous to humans.

A small number of additional uses for species of *Buddleja* are noted in the literature. Buddledin sesquiterpenes (see Yoshida *et al.*), as well as saponins, help to account for utilization of *Buddleja* as fish poison. Wood from species of *Buddleja* has limited utility as fuel. *Buddleja americana* is burned as an incense in the New World (Morton), and at least one other species is used the same way during funeral ceremonies in China (S. Y. Hu, pers. comm.). Tree species yield wood used in construction. Flowers of *B. asiatica* have been cooked with meat and used in wine (Leenhouts, 1962); those from *B. mar-rubiifolia* Benthams have given color to Mexican foods; and "a substitute for saffron" comes from flowers of *B. utilis* Kränzlin (Macbride).

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